

IS FIRE A DISTURBANCE IN GRASSLANDS?

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Abstract. Many grasslands, and in particular the tallgrass prairies of North America, are generally thought to be maintained by periodic fire. Semantic disagreement among researchers, however, threatens to hamper discussion of fire as an ecological force in grassland ecosystems. Some authors emphasize that fires are disturbances (or perturbations) since these fires disrupt or alter ecosystem states, trends, and dynamics (e.g., accumulating nitrogen is volatilized, plant and animal communities change in composition). Other researchers point out that, because these fire-induced disruptions and alterations can maintain the status quo of the ecosystem (e.g., prevent it from becoming woodland), it is the lack of fire rather than fire itself that should be considered a disturbance. We argue that, since both points of view are useful, there is little to be gained by labeling loosely either fire or the lack thereof as a "disturbance" in grassland ecosystems.

Key Words. disturbance, fire, grasslands, perturbation, prairie, Kansas

INTRODUCTION

Recurrent fire is widely regarded as an important, natural phenomenon of many ecosystems (Mooney *et al.* 1981, Wright and Bailey 1982), including many of the world's grasslands (Vogl 1974, Kucera 1981, Anderson 1982, Axelrod 1985). Towne and Owensby (1984), for example, succinctly state the general sentiment that tallgrass prairie of North America is "fire-derived and fire-maintained." But a semantic problem is surfacing in the grass-

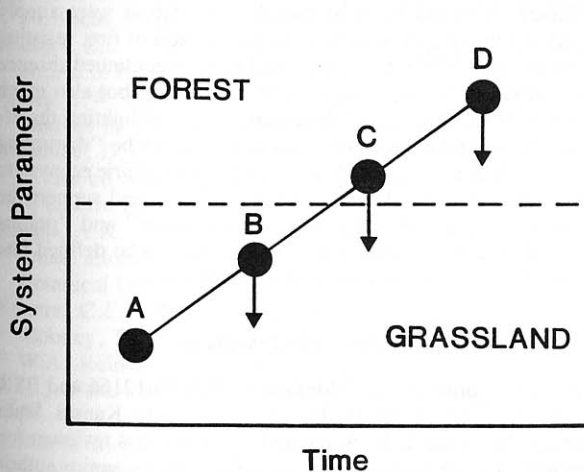


FIG. 1. Graphical illustration of the effect of fire upon system (ecosystem or community) parameters (e.g., biomass of grass tissue). The approximate bounds between a grassland and forest system are shown by the hatched line. The original state of the system is at position A, within the bounds of the grassland. Without fire, through time the system tends towards forest. A fire at B disrupts the system, but it remains as grassland; this could be repeated indefinitely. Without fire the system moves towards C, becoming forest. At C, a fire (of intensity as at B) moves the system back to grassland. In the continued absence of fire, the system reaches D, where after a fire of similar intensity the system remains a forest.

land literature that threatens to hamper understanding of how fire functions in ecosystems.

At issue is whether fires in grasslands (and other ecosystems) should or should not be considered (natural) disturbances/perturbations. Authors disagree more in semantics than in ecological substance. In fact, their disparate studies of nitrogen dynamics, plant succession, and grasshopper assemblages are linked conceptually by two common themes regarding grassland fires. Focus on one theme leads some researchers to label grassland fires as disturbances (Evans 1984, Collins and Barber 1985, Pickett and White 1985, and Collins 1987), while focus on the second theme leads other researchers to the opposite position, namely that it is the lack of fire that is the disturbance (Hulbert 1969, Lamotte 1983, van Andel and van den Bergh 1987).

The two themes can be stated simply. On the one hand, grassland fires disrupt or alter ecosystem states, trends, and dynamics. Accumulating nitrogen is volatilized (Seastedt 1988), expanding woody plant populations are reduced (Knapp 1986, Abrams and Hulbert 1987, Gibson and Hulbert 1987), animal communities change in composition (Kaufman *et al.* 1983, Evans 1984, Seastedt 1984a and 1984b, James 1988). These kinds of changes lead some researchers to label grassland fires as disturbances. On the other hand, these fire-induced disruptions and alterations can maintain the status quo of the ecosystem by preventing it from drifting beyond the loose bounds within which ecologists consider the ecosystem a grassland and outside of which it is recognized as a different system (Figure 1). The long-term result of the absence of fire in the North American tallgrass prairie region, for example, is the transformation of grassland to deciduous forest (Bragg and Hulbert 1976). It is this type of shift that leads some ecologists to view the absence rather than the occurrence of fire as a disturbance (White 1987).

Semantic difficulties arise in part from somewhat separate intellectual traditions. Ecosystem ecologists have used the terms disturbance and perturbation in comparing systems with differing degrees of what is now widely termed neighborhood stability. The system response to perturbation (used as a more neutral term than disturbance) has been described in terms of resistance and resilience (Webster *et al.* 1975, Swank and Waide 1980). This approach formally recognizes differences between the specific forcing function (the perturbation) and the system response. Lewis (1969) discussed state or controlling factors *vs.* dependent factors in ecosystems. As long as forcing variables such as climate do not deviate beyond a range of values, the system exhibiting neighborhood stability remains about the same. For example, Godron and Forman (1983) state that disturbance is "something that causes a community or ecosystem characteristic, such as species diversity, nutrient output, biomass, vertical or horizontal structure to exceed or drop below its common (homeostatic) range of variation." In this framework, the lack of fire can be usefully viewed as a disturbance to the grassland system. The tallgrass prairie without fire, for example, lacks both resistance (it takes no change in climate to change the system) and resilience (it does not return to its present state without fire). Ultimately, however, one's perception of stability and/or disturbance depends upon properties of the system as well as the forcing function, as illustrated for grasslands and fire in Figure 2.

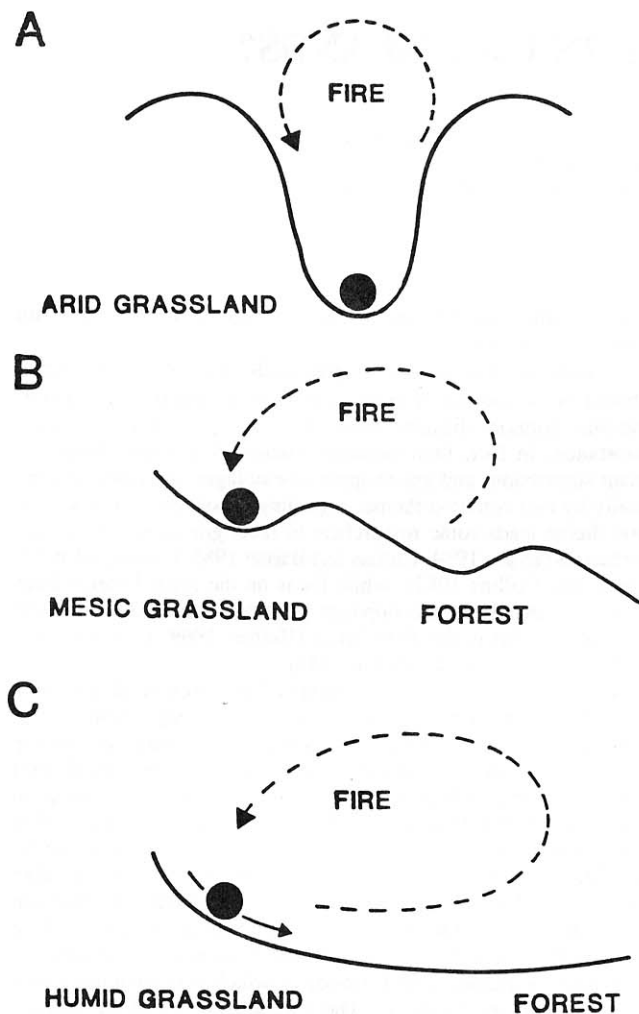


FIG. 2. The influence of fire depends upon the intrinsic properties of the system, as well as other external inputs. In (A) an arid grassland (e.g., shortgrass prairie) remains a grassland regardless of the presence or absence of fire. In (B) a grassland (e.g., mixed grass prairie in some cases) may be invaded by woody species if a seed source is available. The same climatic variables may support either system (a case of multiple stable points), but fire will drive the system to a grassland. In (C) a humid grassland (e.g., tallgrass prairie), with moist climate and woody seed sources present, is converted to forest unless fire intervenes.

Population and community ecologists have emphasized disturbance as a useful concept (Pickett and White 1985) in analyzing how interacting organisms respond to change in the resource bases of ecosystems. Fire is viewed as a naturally-occurring, interactive component of the complex of processes that characterize both grasslands (Loucks *et al.* 1985, Collins 1987, Evans 1988a and 1988b) and communities in general (Sousa 1984, Pickett and White 1985).

These schools of thought have encountered difficulty addressing the diversity of organism and system responses and the attendant problems of scale in deriving a robust operational definition of disturbance/perturbation. Allen and Wyleto (1983) demonstrate, for example, how analyses of different aspects of a single data base can lead to opposing conclusions regarding how fire affects an ecosystem. Both Allen and Starr (1982) and O'Neill *et al.* (1986) emphasize that whether or not fire will be considered a disturbance depends not only on one's definition of disturbance

but also on the spatial and temporal scales on which one chooses to focus. These difficulties compound those of joining the frames of reference of diverse ecological perspectives to derive a single, all-encompassing definition of disturbance and perturbation.

Misunderstanding surrounding use of the terms disturbance and perturbation arises because many individuals carry with them some firmly held "psychological baggage." The root of the problem probably lies in a cultural and philosophical predisposition to attach negative connotations to the term disturbance. In a scientific tradition that has generally embraced a gradualist view of change in the earth's geological and biological processes (e.g., continuous evolution *vs.* punctuated equilibria), a disturbance is something outside of the proper train of events. We speak of some individuals as "mentally disturbed;" riots are referred to as "disturbances." Thus, to label an integral ("natural") aspect of an ecosystem, such as fire in grasslands, a "disturbance" may be disquieting, since a disturbance should be something "unnatural." From this viewpoint, labeling a fire as a "natural disturbance" only confuses the issue, as the phrase seemingly is a contradiction in terms. Certainly most would reject the idea that their thoughts were so subjective, but can anyone be sure that years of conditioning do not color one's thought (Mayr 1982)? Perhaps ecologists of a culture with a more revolutionary or cyclical world-view might not have negative associations with labels used for recurrent catastrophes. However, recent developments in evolution and ecology such as the theory of punctuated equilibria (Eldredge 1985), chaos theory (May and Seger 1986), and increased interest in analysis of non-equilibrium situations (Houston 1979), are evidence that ways of thought are changing.

Given these various considerations, it is not surprising that a useful definition of ecological disturbance rising above semantic difficulties has proved elusive (White 1979, Bazzaz 1983, Godron and Forman 1983, Sousa 1984, Pickett and White 1985, Rykiel 1985, van Andel and van den Bergh 1987). Neither is it surprising that there is lack of agreement regarding inclusion/exclusion of grassland fires in particular as disturbances. Good semantic arguments can be made either for or against grassland fire as a natural disturbance. It would be most useful if the debate were simply dropped and investigators focused on the impacts of fire, resisting the temptation to label either grassland fire or its continued absence as a disturbance. A potentially less inflammatory (but also much less inspired) substitute for "disturbance" in highlighting the effects of fire on grassland ecosystems might simply be "disrupting influence." In any case, our studies of a tallgrass prairie ecosystem illustrate the diversity of biotic responses to fire and support the position that facile use of the terms "disturbance" and "perturbation" should be avoided. These words need to be defined and used carefully in any discussion of grassland fires.

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LITERATURE CITED

- Abrams, M.D., and L.C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *American Midland Naturalist* 117:442-445.
- Allen, T.F.H., and T.B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago.
- Allen, T.F.H., and E.P. Wyleto. 1983. A hierarchical model for the complexity of plant communities. *Journal of Theoretical Biology* 101:529-540.

- Anderson, R.C. 1982. An evolutionary model summarizing roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. Pages 297-308. In J.R. Estes, R.J. Tyrl and J.N. Brinken (eds.). Grasses and grasslands: systematics and evolution. Oklahoma University Press, Norman.
- Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:163-201.
- Bazzaz, F.A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. Pages 259-275. In H.A. Mooney and M. Godron (eds). Disturbance and ecosystems. Components of response. Springer-Verlag, Berlin.
- Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management* 29:19-24.
- Collins, S.L. 1987. Interaction of disturbance in tallgrass prairie: a field experiment. *Ecology* 68:1243-1250.
- Collins, S.L., and S.C. Barber. 1985. Effects of disturbance in mixed-grass prairie. *Vegetatio* 64:87-94.
- Eldredge, N. 1985. Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York.
- Evans, E.W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. *Oikos* 43:9-16.
- Evans, E.W. 1988a. Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? *Oikos* 52:283-292.
- Evans, E.W. 1988b. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography, and vegetation. *Canadian Journal of Zoology* 66:1495-1501.
- Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography, and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:175-185.
- Godron, M., and R.T.T. Forman. 1983. Landscape modification and changing ecological characteristics. Pages 12-28. In H.A. Mooney and M. Godron (eds.). Disturbance and ecosystems. Components of response. Springer-Verlag, Berlin.
- Houston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 133:81-101.
- Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* 50:874-877.
- James, S.W. 1988. The post-fire environment and earthworm populations in tallgrass prairie. *Ecology* 69:476-483.
- Kaufman, D.W., G.A. Kaufman, and E.J. Finck. 1983. Effects of fire on rodents in tallgrass prairie of the Flint Hills Region of eastern Kansas. *Prairie Naturalist* 15:49-56.
- Knapp, A.K. 1986. Postfire water relations, production, and biomass allocation in the shrub, *Rhus glabra*, in tallgrass prairie. *Botanical Gazette* 147:90-97.
- Kucera, C.L. 1981. Grassland and fire. Pages 90-111. In H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds.). Fire regimes and ecosystem properties. U.S. Forest Service, Washington, D.C. Technical Report Wo-26.
- Lamotte, M. 1983. Research on the characteristics of energy flows within natural and man-altered ecosystems. Pages 48-70. In H.A. Mooney and M. Godron (eds.). Disturbance and ecosystems. Components of response. Springer-Verlag, Berlin.
- Lewis, J.K. 1969. Range management viewed in the ecosystem framework. Pages 97-187. In G.M. Van Dyne (ed.). The ecosystem concept in natural resource management. Academic Press, New York.
- Loucks, O.R., M.L. Plum-Mentjes, and D. Rogers. 1985. Gap process and large-scale disturbances in sand prairies. Pages 72-84. In S.T.A. Pickett and P.S. White (eds.). The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- May, R.M., and J. Seger. 1986. Ideas in ecology. *American Scientist* 74:256-267.
- Mayr, E. 1982. The growth of biological thought: diversity, evolution and inheritance. Belknap Press, Cambridge, Massachusetts.
- Mooney, H.A., T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners, (eds.). 1981. Fire regimes and ecosystem properties. U.S. Forest Service Technical Report Wo-26.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A hierarchical concept of ecosystems. *Monographs in Population Biology*, 23, Princeton University Press, Princeton, New Jersey.
- Pickett, S.T.A., and P.S. White (eds.). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- Rykiel, E.J. 1985. Toward a definition of ecological disturbance. *Australian Journal of Ecology* 10:361-365.
- Seastedt, T.R. 1984a. Belowground macroarthropods of annually burned and unburned tallgrass prairie. *American Midland Naturalist* 111:405-408.
- Seastedt, T.R. 1984b. Microarthropods of burned and unburned tallgrass prairie. *Journal of the Kansas Entomological Society* 57:468-476.
- Seastedt, T.R. 1988. Mass, nitrogen and phosphorus dynamics in foliage and root detritus of annually burned and unburned tallgrass prairie. *Ecology* 69:59-65.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Swank, W.T., and J.B. Waide. 1980. Interpretation of nutrient cycling research in a management context: evaluating potential effects of alternative management strategies on site productivity. Pages 137-158. In R.W. Waring (ed.). Forests: fresh perspective from ecosystem analysis. Oregon State University Press, Corvallis.
- Towne, G., and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *Journal of Range Management* 37:392-397.
- van Andel, J., and J. P. van den Bergh. 1987. Disturbance of grasslands. Outline of the theme. Pages 3-13. In J. van Andel, J.P. Bakker, and R.W. Snaydon (eds.). Disturbance in grasslands. Dr. W. Junk, Netherlands.
- Vogl, R. 1974. Effects of fire on grasslands. Pages 139-194. In T.T. Kozlowski and C.E. Algren (eds.). Fire and ecosystems. Academic Press, New York.
- Webster, J.R., J.B. Waide, and B.C. Patten. 1975. Nutrient cycling and the stability of ecosystems. Pages 1-27. In F.G. Howell, J.B. Gentry, and M.H. Smith (eds.). Mineral cycling in southeastern ecosystems. Energy Research and Development Administration Symposium Series (Conf-740SB), National Technical Information Service, Springfield, Virginia.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- White, P.S. 1987. Natural disturbance, patch dynamics and landscape pattern in natural areas. *Natural Areas Journal* 7:14-22.
- Wright, H.A., and A.W. Bailey. 1982. Fire ecology. Wiley-Interscience, New York.

